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Pteropus hypomelanus. By Deborah P. Jones and Thomas H. Kunz

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Pteropus Erxleben, 1777

Pteropus Erxleben, 1777:130. Type Pteropus niger Kerr, 1792. Spectrum Lacépède, 1779:15. Type Pteropus niger Kerr, 1792. Preoccupied by Spectrum (a lepidopteran) Scopoli, 1777.

Eunycteris Gray, 1866:64. Type Pteropus phaiops Temminck (= Pteropus melanopogon Peters, 1868:626).

Pselaphon Gray, 1870:110. Type Pteropus pselaphon Layard, 1829.

Sericonycteris Matschie, 1899:30. Type Pteropus subniger Kerr, 1792.

Desmalopex Miller, 1907:60. Type Pteropus leucopterus Temminck, 1853.

CONTEXT AND CONTENT. Order Chiroptera, suborder Megachiroptera, family Pteropodidae, genus *Pteropus. Pteropus* currently includes 58 species (Koopman, 1993). Andersen's (1912) key to the genus *Pteropus* is outdated. Ingle and Heaney (1992) included *Pteropus* in a key to bats of the Philippines, but no recent key includes all members of the genus.

Pteropus hypomelanus Temminck, 1853

Small-island Flying Fox

Pteropus hypomelanus Temminck, 1853:61. Type locality "Ternate Islands," North Molucca, Indonesia.

Pteropus condorensis Peters, 1869:393. Type locality "Pulo Condore," (= Con Son, Vietnam).

Pteropus tricolor Gray, 1870:108. Type locality "Ternate Island," North Molucca, Indonesia.

Pteropus macassaricus Heude, 1897:177. Type locality "Macassar," South Sulawesi, Indonesia.

Pteropus lepidus Miller, 1900:237. Type locality "Kaju Ara, or Saddle Island, Tambelan Islands," Indonesia.

Pteropus geminorum Miller, 1903:60. Type locality "South Twin Island, Mergui Archipelago," Burma.

Pteropus cagayanus Mearns, 1905:433. Type locality "Cagayan Sulu Island," Philippines.

Pteropus enganus Miller 1906:822. Type locality "Pulo Dua, near Engano Island," West Sumatra, Indonesia.

CONTEXT AND CONTENT. Context as for genus. Koopman (1994) listed 15 subspecies of *P. hypomelanus*, but we follow Corbet and Hill (1992) who recognized 7 with type localities.

- P. h. annectens Andersen, 1908:361. Type locality "Sirhassen," South Natura Islands, Indonesia.
- P. h. canus Andersen, 1908:361. Type locality "Pulau Pandak, North Natuna Islands," Indonesia.
- P. h. fretensis Kloss, 1916:247. Type locality "Palau Jarak, Straits of Malacca," West Malaysia.
- P. h. maris Allen, 1936:343. Type locality "Heratara, Addu Atoll," Maldive Islands.
- P. h. robinsoni Anderson, 1909:534. Type locality "Rumbia Island, Straits of Malacca," West Malaysia.
- P. h. simalurus Thomas, 1923:592. Type locality "Tapah Island, near Simalur," West Sumatra, Indonesia.
- P. h. var. tomesi Peters, 1868:626. Type locality "Sarawak auf Borneo."

DIAGNOSIS. Length of forearm, overall body size, and locality generally are useful characters for differentiating members of the genus *Pteropus* (Andersen, 1912). *P. hypomelanus* is the largest member of the *hypomelanus* species group, as first designated by Andersen (1912) and later by Corbet and Hill (1992). A naked

dorsal tibia (Klingener and Creighton, 1984) also delineates members of the hypomelanus group. Within this group, P. hypomelanus is distinguished from P. faunulus by its larger body size, larger teeth, and shorter fur (Andersen, 1912; Corbet and Hill, 1992). P. griseus has a shorter length of forearm (<118 mm), a shorter cm2 length (<19.8 mm), and paler pelage than P. hypomelanus (Andersen, 1912). P. dasymallus has a length of forearm (125-140 mm) similar to that of P. hypomelanus (121-150 mm), but a shorter greatest length of skull (59.0-62.5 mm) than P. hypomelanus (62.1–69.0 mm); P. dasymallus also has longer and denser pelage than P. hypomelanus, and unlike P. hypomelanus, has fur on the upper surface of its hind limbs (Ingle and Heaney, 1992). P. hypomelanus is smaller than P. alecto, P. conspicillatus, P. macrotis, and P. neohibernicus (Flannery, 1990). Length of forearm of P. hypomelanus (<150 mm) and condylobasal length (<65 mm) distinguish it from P. vampyrus (length of forearm >165 mm and condylobasal length >68 mm). A pale patch of fur on the chest distinguishes P. hypomelanus from the gold-colored form of P. vampyrus (Ingle and Heaney, 1992; Payne et al., 1985). P. hypomelanus is larger than P. pumilus (with a length of forearm <113 mm and a condvlobasal length <52 mm), and hairs on the throat of P. hypomelanus are dark brown instead of pale gray as in P.



FIG. 1. Female *Pteropus hypomelanus* from Indonesia, housed in captivity at The Lubee Foundation, Inc., Gainesville, Florida. Photograph by T. H. Kunz.

pumilus (Ingle and Heaney, 1992). *P. hypomelanus* is distinguished from *Dobsonia chapmani* by having a claw on the second digit and by having four upper and two lower incisors (Ingle and Heaney, 1992).

GENERAL CHARACTERS. Body of *P. hypomelanus* is fully furred (Fig. 1). Hair on pinna is long and sparse anteriorally, but upper half of posterior surface of ear is nearly naked. Hair on forehead is short and dense and gradually becomes longer from neck to mantle. Dorsal fur is relatively short and adpressed, and ventral fur is of medium length (Andersen, 1912; Taylor, 1934). Wing membranes are attached along midline of the back (Bergmans and Rozendaal, 1988; Taylor, 1934) and at base of first phalanx of second toe (Taylor, 1934).

Fur color in *P. hypomelanus* is highly variable. Typically, fur on head is dark brown, although in some individuals it fades to light brown or yellowish brown. Mantle (fur around neck) varies in color from pale yellow to darker shades of brown and gradually darkens from east to west across the distributional range. Dorsum is brownish to reddish brown, although in some subspecies silver or gray hairs occur. Venter ranges from golden ocherous buff to cream buff in color; in some individuals venter is darker. Flanks have the same dark brownish color as back (Kula, 1992). Hairs around eyes are often grayish in color (Lekagul and McNeely, 1977). In some subspecies, two color phases occur in which pelage has a blackened or a gray-blackish grizzled pattern (Andersen, 1912). Hair scales of *P. hypomelanus* are 14.0 μm wide and 18.3 μm long (Gaisler and Barus, 1978).

Ranges of external and cranial measurements (in mm) are: length of forearm, 121-150; total length, 183-240; length of hind foot, 39-55; length of ear from notch, 28-32; length of pollex, 54.0-62.5; length of metacarpal of pollex, 12.0-14.5; length of phalanx I of pollex, 28-33; length of metacarpal of digit II, 62.5-74.5; length of phalanx of digit I, 14.0-18.5; length of phalanx of digit II-III, 13-18; length of metacarpal of digit III, 82.0-97.5; length of phalanx I, 61.5-71.0; length of phalanx II, 87-106; length of metacarpal of digit IV; 80-95; length of phalanx I, 50.5-58.5; length of phalanx II, 47.5-60.0; length of metacarpal-digit V, 87-102; length of phalanx I, 37.0-43.5; length of phalanx II, 36-46; distance from front of eye to tip of muzzle, 25.5-27.5; length of interfemoral membrane, 0-4; length of tibia, 54.5-65.0; length of calcar, 12.5-17.5; greatest length of skull, 62.1-69.0; condylobasal length, 57.6-65.0; zygomatic breadth, 30.6-38.5; width of braincase, 21.8-24.2; width of braincase at zygomata, 34.2-36.9; mastoid width, 19.0-20.8; length of palate to incisive foramina, 30-35; width of maxillary toothrow, 23.0-25.6; length of molariform toothrow, 15.5-16.4; width across M1, externally, 16.5-19.0; width across canines, externally, 11.6-14.0; lachrymal width, 11.6-15.7; width of postorbital constriction. 6.8-9.2: width of interorbital constriction, 8.0-10.0; orbital diameter, 11.4-13.2; width of mesopterygoid fossa, 7.0-8.2; width of palate between P4 and P4, 9.0-11.7; width between cingula of canines, 6.4-7.9; length of mandible, 47.7-54.7; height of coronoid process, 20.7-26.2; length of C-M2, 21.8-27.5; and length of c-m3, 24.6-30.2 (Andersen, 1912; Bergmans and Rozendaal, 1988; Corbet and Hill, 1992; Heaney, 1984; Heaney and Rabor, 1982; Ingle and Heaney, 1992; Sanborn and Beecher, 1947; Thomas, 1915; Van Peenen et al., 1969, 1970). In the Philippines, body mass ranges from 425 to 450 g (Ingle and Heaney, 1992).

Cranium of *P. hypomelanus* is large, elongate, and robust, with well-developed postorbital processes and a bony spur on anterior surface of zygomatic arch (Fig. 2). Temporal ridges are fused, often forming a high sagittal crest.

Pteropus hypomelanus lacks a bony patella, but has a fibrocartilage and hyaline cartilage within quadriceps tendon (Smith et al., 1995). Quadriceps tendon forms from dense regular connective tissue on the superficial surface of the quadriceps. A pad of hyaline cartilage similar to articular cartilage is found on the deep surface of the tendon. This cartilage adjoins a layer or "herringbone" fibrocartilage, in which large bundles of collagen fibers are located at acute angles to each other. Distally, the fibrocartilaginous layer of connective tissue eventually blends with normal, dense connective tissue that forms the bulk of the tendon (Smith et al., 1995).

DISTRIBUTION. *Pteropus hypomelanus* has a widespread, but fragmented, distribution in the Indo-Australian region (Fig. 3). Its distributional range, greater than other members of the genus



FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of a male *Pteropus hypomelanus* from Panay, the Philippines (National Museum of Natural History [USNM] 105443). Greatest length of skull (without incisors) is 66.0 mm. Drawings from Ingle and Heaney (1992); reprinted with permission of the Field Museum.

Pteropus, extends from the Indo-Australian Archipelago, Papau New Guinea, Trobriand and Woodlark Islands, and westward to Thailand and the Mergui Archipelago, excluding Java and the lesser Sunda Islands (Andersen, 1912). This species also occurs in the Maldives, but not in India or Sri Lanka. *P. hypomelanus* has not been reported from the mainland of the Malaya Peninsula, although populations are known from islands along eastern and western coastal regions of the peninsula (Hill and Thonglongya, 1972; Lim, 1966). In Papua New Guinea, *P. hypomelanus* occurs off the northern coast, where it roosts on small islands, but it is rare on the mainland (Flannery, 1990; Koopman, 1979; Lim, 1966). Flannery (1990) and Nowak (1991) list *P. hypomelanus* as occurring in the Solomon Islands, but no recent records exist of its occurrence on



FIG. 3. Geographic distribution of *Pteropus hypomelanus*. Map redrawn from Corbet and Hill (1992). Current subspecific distributions are not well defined.

these islands. In the Philippines, this bat occurs from sea level to >900 m, but it is rare in both montane upland forest and submontane rainforest (Heaney et al., 1981; Heideman and Heaney, 1989). In the Conflict Islands, the species is only known from elevations <100 m (Bergmans and Rozendaal, 1988; Heideman and Heaney, 1992; Koopman, 1982). *P. hypomelanus* has no fossil record.

FORM AND FUNCTION. Dental formula of P. hypomelanus is i 2/2, c 1/1, p 3/3, m 2/3, total 34 (Andersen, 1912). Upper incisors are arranged in a semicircle and are well separated from canines (Andersen, 1912; Lekagul and McNeely, 1977). Canines are strong, stout, and have a deep longitudinal groove on anterior surface (Andersen, 1912). Upper canines are distinctly recurved and cingulum is moderate, forming a well-defined, but narrow, ridge at inner and posterior base. Upper incisors form a semicircle, well separated from the canine. Lower canines are recurved, with a moderate cingulum (Andersen, 1912). P1 is minute, peglike, and often absent in adults (Andersen, 1912; Lekagul and McNeely, 1977). Premolars have a distinct ridge on posterior surface (Lekagul and McNeely, 1977). The M1 and M2 lack antero-internal cusps and inner basal ledges, and m1 and m2 lack inner basal ledges (Bergmans and Rozendaal, 1988). Palatal ridge formula (5 + 5 + 3)includes an occasional extra ridge between ninth and 10th ridges. The first ridge terminates laterally in front of canines, the second at the back of canines, followed by the third in front of P3, fourth at back of P3, fifth at P4, sixth at front of M1, seventh at back of M1, eighth at M2, ninth and 10th behind M2, and 11th to 13th at palatal border (Andersen, 1912).

As measured in captive animals, *P. hypomelanus* has among the highest circulating basal levels of adrenal steroids recorded for any mammal (\pm *SE*): cortisol 1,269 \pm 207 ng/ml and corticosterone 590 \pm 154 ng/ml. Cortisol remains relatively constant throughout the day-roosting period and declines to the lowest diel level after food intake (Widmaier and Kunz, 1993). Plasma levels of glucose in unstressed *P. hypomelanus* fall within the normal mammalian range (80–100 mg/dl), with no differences between sexes. Glucose reaches a minimum level immediately before and a maximum level just after food intake. Handling and isolation cause significant increases in both plasma cortisol and glucose levels. Experiments based on 3-h restraint stress caused cortisol levels to increase by 800% after 2 h, with the first significant increase observed within 20 min. Normal total cholesterol level in captive *P. hypomelanus* is $12 \pm 4 \text{ mg/dl} (\pm SE$ —Widmaier et al., 1996). Compared with other mammals, low levels of cholesterol and urea in *P. hypomelanus* may be related to its primary diet of fruit (Heard and Whittier, 1997). Lymphocytes were the predominant white blood cells in *P. hypomelanus* (Heard and Whittier, 1997).

Basal metabolic rate of *P. hypomelanus* is $216.2 \text{ cm}^3 \text{ O}_2/\text{h}$ (McNab and Bonaccorso, 1995). At low ambient temperatures *P. hypomelanus* lowers its metabolic rate without lowering its core temperature. Temperature of periphery is allowed to drop to near environmental temperature during periods of inactivity (McNab and Bonaccorso, 1995).

Baculum of *P. hypomelanus*, as in other members of the genus, has a saddle-shaped profile when viewed laterally (Krutzsch, 1962; Lanza, 1963). It ranges from 6.2 to 8.2 mm in length, and from 5.3 to 7.3 mm in width, with ratio of length to width ranging from 0.97 to 1.20. Proximal prongs (horns) of baculum are separate, instead of being fused as in other pteropodids; size of medial opening seems to decrease with age. Number of spines on longitudina and transverse spinosa areas ranges from 16 to 24 and 11 to 24, respectively.

Dorsal length and maximum width (mm) of the caput penis

(head of penis) in *P. hypomelanus* ranges from 6.2 to 8.6 mm and from 7.7 to 11.0 mm, respectively. Dorsal aspect typically has a single median spiny area at apex. Characteristics of the caput penis, along with those of the baculum, distinguish two groups within the genus. The caput penis of *P. hypomelanus* has a lateroventral groove at least half the length of the spinous area, but no transverse subapical groove (Lanza, 1963).

Dilated cardiomyopathy was reported in captive *P. hypomelanus*, a condition consistent with decreased myocardial function and development of congestive heart failure (Heard et al., 1996). Related symptoms in these bats included lethargy, reluctance to fly, intolerence to exercise, hypothermia, tachyarrhythmias, hepatomegaly, and cranial edema. Although possible causes of myocarditis include viral, bacterial, fungal, and protozoal infections, ingestion of toxic agents, nutritional deficiencies, trauma, stress, and abnormal clinicopathologic changes, none of these conditions were identified in routine clinical evaluations (Heard et al., 1996; Heard and Whittier, 1997). However, adequate dietary intake of vitamin E apparently is considered important for the prevention of myocardial injury in captive *P. hypomelanus* (Heard et al., 1996).

ONTOGENY AND REPRODUCTION. In the Philippines, pregnant P. hypomelanus occurred in April (Rickart et al., 1993), females gave birth in April and May (Heideman, 1987, 1995), and lactating females occurred in August (Flannery, 1994). Young P. hypomelanus remain dependent on their mothers for at least 3 months (Heideman, 1987, 1995). In the Philippines, reproductive maturity is achieved at the age of 1 year in both sexes (Heideman and Heaney, 1992). In captivity (The Lubee Foundation, Inc., Gainesville, Florida), females gave birth each month of the year, with a peak birth period in May and June (J. Seyjagat, in litt.). At birth, body mass and length of forearm in young P. hypomelanus average 74 g and 62 mm, respectively. These values represent 13.0% and 39.4% of maternal body mass and length of forearm, respectively (Kunz and Hood, in press). Logistic growth constant and asymptotic body mass for captive P. hypomelanus are 0.011 and 515.2 g, respectively. Logistic growth constant (K) and asymptotic size (A) for length of forearm are 0.016 (K, 1/time) and 153.3 mm, respectively (Kunz and Hood, in press).

Dry matter content of milk in *P. hypomelanus* is comparable to other members of the Megachiroptera, averaging 16.5% in early and 18.4% in late lactation (Kunz and Hood, in press). Average percentages of fat, protein, and carbohydrate in milk are 7.6%, 2.5%, and 6.0% early in lactation and 9.4%, 2.9%, and 5.6% late in lactation, respectively. Energy content of milk from early to late lactation averages 0.9 and 1.1 kJ/g (wet mass), respectively. Mineral content (ml/g) of milk from *P. hypomelanus* is: Na⁺, 1.56; K⁺, 0.94; Ca²⁺, 1.24; Mg²⁺, 0.09; and P. 1.01 (Kunz and Hood, in press).

ECOLOGY. Pteropus hypomelanus feeds on fruit and nectar obtained from wild and cultivated plant species (Phillips, 1958; Van Peenen et al., 1969), including pawpaw fruit (Carica papaya), mango (Mangifera indica), jambu (Syzygium), occasionally bananas or plantains (Musa), figs (Ficus), banyan flowers (Ficus), berries of the damba tree (Calophyllum inophyllum), and fruits of cultivated crops (Flannery, 1994; Heideman and Heaney, 1992; Phillips, 1958). In the Philippines, P. hypomelanus feeds largely on figs (Utzurrum, 1995). This bat also feeds on flowers of the kapok tree (Ceiba), as well as chico (Pouteria sapota) and coconut flowers (Cocus nucifera—Heideman and Heaney, 1992; Hill and Smith, 1984), and on fruits of the babolo tree (Diospyros—Rickart et al., 1993). In areas where P. hypomelanus is gregarious, as in the Phillippines, several individuals may feed together in the same tree (Heideman and Heaney, 1992).

The small-island flying fox commonly occurs in lowland agricultural habitats where it roosts in fronds of the coconut palm (*Cocus nucifera*—Heideman and Heaney, 1992; Hill and Smith, 1984; Lim, 1966; Marshall and Nongngork, 1970; Medway, 1968; Payne et al., 1985; Phillips, 1958; Rickart et al., 1993; Sanborn, 1952). This species is rarely found in primary forest (Heaney et al., 1989; Heideman and Heaney, 1992). Individuals in urban areas sometimes become entangled in high electrical wires and in support cables of telecommunications towers (Heideman and Heaney, 1992). Little is known about longevity for *P. hypomelanus* in the wild or in captivity, but wild-caught individuals have survived in captivity for at least 9 years (J. Seyjagat, in litt.).

Ectoparasites of the families Laelapidae and Nycteribiidae oc-

cur frequently on *P. hypomelanus*, but in relatively low numbers; members of the family Spinturnicidae are found less often (Beck, 1971). The nycteribiid *Cyclopodia horsfieldi* is known from a single specimen from Ujung Pandang (Bergmans and Rozendaal, 1988). The endoparasite *Makifilaria inderi* (Filarioidea: Onchocercidae) has been reported from the abdominal cavity of *P. hypomelanus* (Krishnasamy et al., 1981), and adults and eggs of nematode *Toxocara pteropodis* (Ascaridoidea) were reported from one of several suckling *P. hypomelanus* born in captivity (Heard et al., 1995). Rectal bacterial flora reported from *P. hypomelanus* include gram-positive rods (Actinomycete and *Corynebacterium*), grampositive cocci (*Enterococcus*, *Micrococcus*, *Staphylococcus*, *Streptococcus*—hemolytic, group D, and nonhemolytic), gram-negative rods (*Escherichia coli*, *Proteus*, *P. mirabilus*), and yeast (Heard et al., 1997).

Pteropus hypomelanus has no natural enemies (Phillips, 1958), but is hunted extensively for food by humans in the Philippines (Heideman and Heaney, 1992) and Malaysia (A. Zubaid, in litt.). The noisy and conspicuous roosting habits of this species often betray its presence, making it susceptible to extermination by hunters. This bat is sometimes exported for food (Wiles, 1992). Because their fur has a strong odor that can affect the flavor of the meat (Lekagul and McNeely, 1977), these bats are usually skinned before cooking.

BEHAVIOR. Pteropus hypomelanus may roost individually or in colonies from 10 to several hundred individuals (Heideman and Heaney, 1992; Hill and Smith, 1984; Phillips, 1958; Rickart et al., 1993). In gregarious roosting situations, colonies are usually organized into small family groups. Paired agonistic encounters at roost sites usually involve threats and boxing with closed wings (Rickart et al., 1993). In the Maldive Islands, *P. hypomelanus* always roosts alone and if two individuals meet while feeding, a "wrangling, screeching interlude ensues" until one of them leaves (Phillips, 1958:336).

Colonies may number from tens to several hundred individuals (Heideman and Heaney, 1992). In the Philippines, colonies of 50–70 bats were evenly dispersed in the crown of coconut (*C. nucifera*) trees (Rickart et al., 1993). In Malaysia, roosting groups typically consist of 40–50 individuals (Lim, 1966). When exposed to the hot sun during the day, these bats often cool themselves by flapping their wings, licking their chest and wings, and panting. In cool weather or during heavy rain, they almost completely wrap themselves with their wings (Lekagul and McNeely, 1977; Ochoa and Kunz, 1999).

Individuals of *P. hypomelanus* may disperse nightly from islands on which they roost to forage on a nearby mainland (Payne et al., 1985; Van Peenen et al., 1970), but none has been captured >6-8 km from a known roost site (Heideman and Heaney, 1992). Individuals fly as high as 30 m above the ground, and when flying across the sea they sometimes seek troughs in waves to avoid wind resistance (Phillips, 1958). In flight, thumb claws are extended rigidly in front of the wing (Phillips, 1958). When an individual alights in a tree, it first lands in a head-up position, grasping the branch with both feet and wing claws, then proceeds to assume a head-down posture. Typically, *P. hypomelanus* feeds in a head-down position but it also may do so with its head held upward (Phillips, 1958).

GENETICS. Diploid and fundamental numbers of *P. hypomelanus* from Negros Islands, Philippines, are 38 and 72, respectively (Rickart et al., 1989). Autosomal complement consists of 10 pairs of metacentric or subcentric chromosomes of small to large size and 8 pairs of subtelocentric chromosomes of small to medium size. The marker chromosome is a submetacentric of medium size; the X chromosome is a subtelocentric of medium size; and the Y is a small acrocentric chromosome (Rickart et al., 1989).

CONSERVATION STATUS. This species is protected in some regions, but is hunted in other parts of its range (Heideman and Heaney, 1992). Along with other members of the genus, *P. hypomelanus* was placed on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) list in 1989.

REMARKS. *Pteropus hypomelanus* formerly included *P. brunneus* (Ride, 1970). Koopman (1984) considered *P. brunneus* to be distinct from *P. hypomelanus*, having been reported as the

type from Perry Island, off the coast of east-central Queensland. Based on similarity, Koopman (1979) combined *P. hypomelanus* and *P. admiralitatum* into a superspecies. Difficulty assigning individuals to subspecies within *P. hypomelanus* may in part reflect its wide geographic range and its predilection for small islands (Corbet and Hill, 1992; Koopman, 1982). However, forms usually are distinguishable by differences in size and color (Andersen, 1912).

Common names for *P. hypomelanus* vary among islands and include island flying fox, Condoro Island flying fox, variable flying fox, lesser flying fox, kluang kechil, kalong kecil, memboi, or udawed. The generic name *Pteropus* means 'wing-footed' (Gove, 1983). It is derived from the Greek words *pteron* meaning 'wing,' 'feather,' or 'fin' (Brown, 1954) and *pous* meaning 'foot' (Gove, 1983). The specific name *hypomelanus* is from the Greek words *hypo*, which means 'below' or 'beneath,' and *melan*, meaning 'blackish' or 'dark' (Brown, 1954; Gove, 1983).

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